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Microalgal availability and consumption by *Siphonaria pectinata* (L., 1758) on a rocky shore

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ABSTRACT

Siphonaria pectinata (L., 1758) is a pulmonate gastropod of the order Basommatophora, which has adopted a lifestyle superficially similar to that of patellogastropod limpets, and is thus often referred to as a «false limpet». In this paper, we present the results of a study investigating microalgal availability and resource utilization by this species in its intertidal habitat, on a rocky shore off Gibraltar (southern Iberian Peninsula).

A number of different experiments are described, which serve to provide an overview of the main food types and their relative availability to this species. These include the sampling of the surface microbial algal film, scanning electron microscopy (SEM) and light microscopy of rock chips and slurry, radular structure, gut contents and faecal pellets.

The results of this study suggest that *S. pectinata* does not feed on encrusting «hard» algae, but rather uses its fine-toothed radula to graze superficial, soft algae, including spores and emerging germlings. We suggest that such a feeding strategy would allow it to reduce competition with other patellogastropod limpets, which tend to scrape deeper into the rocky substrate while foraging. Possible avenues for further research are discussed.

Keywords: *Siphonaria pectinata*, feed, microalgae.

RESUMEN

Disponibilidad y consumo de microalgas por parte de* Siphonaria pectinata *(L., 1758) en un litoral rocoso

Siphonaria pectinata *(L., 1758) es un gasterópodo pulmonado del orden Basommatophora que ha adoptado un modo de vida parecido al de los patelogasterópodos o lapas por lo que, a menudo, se le denomina «falsa lapa». En este trabajo presentamos los resultados de un estudio sobre la disponibilidad y la utilización de las microalgas por esta especie, en su hábitat intermareal, en un litoral rocoso de Gibraltar (al sur de la península Ibérica).*

Se describen diferentes experimentos que proporcionan una visión general sobre los principales alimentos y su disponibilidad. Estos experimentos incluyen el muestreo de una película de algas microscópicas y microscopía electrónica y óptica de lascas y manchas rocosas, rádulas, contenidos intestinales y heces fecales.

Los resultados sugieren que S. pectinata *no se alimenta de algas fuertemente incrustadas sino que más bien utiliza su delicada y dentada rádula para raer las algas blandas superficiales, incluyendo las esporas y las células germinales recién aparecidas. Creemos que esta estrategia de alimentación permite reducir la competencia con otros patelogastrópodos que tienden a raspar el sustrato rocoso más profundo cuando forrajean. Se discuten posibles vías para una futura investigación.*

Palabras clave: Siphonaria pectinata*, alimentación, microalgas.*

INTRODUCTION

The microbial film coating the surface of rocks is an important ecological component of shore communities (Underwood, 1979; Hawkins and Hartnoll, 1983; Hawkins *et al.*, 1989; Hill and Hawkins 1990, 1991, Della Santina *et al.* 1993; Williams, 1993a). Diatoms, bacteria and protozoa all form part of this film; moreover, it is the first attachment site for all macroalgal propagules which settle and germinate in and on it (Wahl, 1989). Biofilm is the principal food resource of microphagous grazers, whose grazing activities can control or even prevent macroalgal recruitment and growth (Underwood, 1979; Lubchenco and Gaines, 1981; Underwood and Jernakoff, 1981; Hawkins and Hartnoll, 1983; Beovich and Quinn, 1992; Iwasaki, 1993; Dye, 1993, 1995; Liu, 1993; Williams, 1993a,b).

Although there is only limited information regarding which components of the biofilm are ingested by microphagous grazers on natural rock surfaces, some work has been done analysing the gut contents of different gastropod species in relation to food availability (Raffaelli, 1995; Croudace, 1987; Little *et al.*, 1990; Hill and Hawkins, 1991; Della Santina *et al.*, 1993), and determining the relationship between seasonal patterns of microalgal availability and dietary intake in several grazing species (Lubchenco and Menge, 1978; Hruby and Norton, 1979; Hill and Hawkins, 1991; Della Santina *et al.*, 1993).

Several authors have also reported on the relative feeding abilities of *Siphonaria* compared to other gastropods, and how their radular structure, which consists of numerous small teeth, apparently renders them incapable of excavating the rock surface, thus limiting their diet to macroalgae (see review by Branch, 1981; Underwood and Jernakoff, 1981; Hawkins and Hartnoll, 1983; Black, Lymbery and Hill, 1988; Beovich and Quinn, 1992; Iwasaki, 1993; Dye, 1995). The upper midlittoral shore of Gibraltar is generally devoid of macroalgae, and the results of the foraging investigations described in Ocaña and Emson (1999a) indicate that *Siphonaria pectinata* (L., 1758) forages over what appears to be bare rock, since it was never observed feeding on macroalgae lower down the shore. The assumption is, therefore, made that *S. pectinata* feeds on components of the microbial film.

For the present paper, the composition of the microbial film on the upper midlittoral zone of the North Mole site (described in Ocaña and Emson, 1999a,b) was studied with reference to temporal changes in its composition and possible ingestion by *S. pectinata*. The gut contents, faeces and radular structure of *S. pectinata* were also examined in an attempt to determine its diet.

MATERIALS AND METHODS

Composition of microbial film

Three rock chips, approximately 2 cm × 2 cm × 0.5 cm, were collected from the substratum, using a hammer and chisel, of rock surface near *S. pectinata* individuals on the upper midlittoral (0.5-0.75 m above MLW). This was repeated at monthly intervals from August 1993 to August 1995. The chips were immediately placed in labelled specimen tubes containing a 10 % formalin-seawater solution and stored in a dark place until ready to be examined. In the laboratory, the rock chips were carefully blotted using tissue paper and were left to dry on labelled Petri dishes at room temperature for 24 h. Smaller fragments, approximately 1 cm × 1 cm, of the dried rock chips were chiselled off and affixed to metal stubs using araldite adhesive. The specimens were coated in gold and observed under a JEOL 25S Scanning Electron Microscope (SEM). The rock chips were first scanned at a magnification of ×700, and whenever algae were observed, they were subsequently examined in greater detail at higher magnifications. This sampling technique was similar to that used by MacLulich (1986) and Hill and Hawkins (1990, 1991). Micrographs of the structures observed were taken for identification.

In addition, an area of rock surface from around the *S. pectinata* individuals measuring approximately 5 cm × 5 cm was scrubbed with a toothbrush and scraped using a knife until no further discoloration due to algal growth could be discerned. The rock slurry which accumulated on the toothbrush and knife was transferred into labelled specimen tubes containing a 10 % formalin-seawater solution and stored in darkness prior to examination. This technique was very similar to that used by MacLulich (1986). In the laboratory, some of the rock slurry was pipetted onto a slide. The calcium carbonate component was then dissolved using 1M hydrochloric acid. A few drops of distilled water were then added to wash out the acid, and the slurry was gently covered with a cover-slip and examined under an

Olympus Vanox light microscope. Photographs of the structures observed were taken for identification.

Radular structure

The radulae of 10 *S. pectinata* specimens, each 10-15 mm long, were examined. The animals were collected while foraging and immediately placed in formalin. The radulae were dissected, washed in distilled water and air-dried at room temperature for 24 h, then flattened onto metal stubs, coated with gold, and examined under the SEM.

Gut content analysis

Twenty actively foraging animals were collected, at two-monthly intervals, from August 1994 to August 1995. These animals were immediately fixed in a 10 % formalin-seawater solution to prevent any further digestion of ingested matter, as in Beovich and Quinn (1992) and Della Santina *et al.* (1993). The gut of each animal was later dissected (in November 1994 and November 1995) and the contents removed and placed on a slide. Any calcium carbonate component was dissolved as described above. After washing out the acid with distilled water, the material was covered with a cover-slip and examined under an Olympus Vanox light microscope. Photographs of structures observed were taken for identification.

Faecal pellet analysis

In order to determine whether benthic diatoms formed part of *S. pectinata*'s diet, faecal pellets were examined for evidence of silicaceous frustules, which are believed to remain largely undigested and for the most part intact and easily identifiable (Hill and Hawkins, 1991; Beovich and Quinn, 1992). Faecal pellets were collected every two months between August 1994 and August 1995 by placing live limpets in containers with sea water for 12 hours. This had previously been found effective by Black, Lymbery and Hill (1988) and Beovich and Quinn (1992). The pellets were collected and placed in a 10 % formalin-seawater solution until ready to be processed in the laboratory. The pellets were washed in distilled water and air-dried at room temperature for 24 h, then flattened onto metal stubs, coated with gold, and examined under a JEOL 25S SEM. The faecal smears were first scanned at a magnification of ×700 and subsequently at higher magnifications whenever any relevant structures were observed. Micrographs of any structures observed were taken for identification purposes.

RESULTS

Composition of microbial film

Table I shows the composition of the microbial film. On the whole, the three rock chips and toothbrushings/scrapings taken each month yielded very little algal material.

On average 25-50 % of the rock chips collected monthly and examined under the SEM were found to be devoid of any recognisable algal forms. The rock slurry derived from toothbrushings and scrapes of grazed (control) rock surface contained large amounts of detritus. Occasionally very tiny fragments of juvenile *Blidingia* spp. (figure 1), *Bangia* spp. (figure 2) and *Calothrix* spp. (figure 3) were found. Unidentified filamentous green (figure 4) and blue-green algae (figure 5) were also observed along with the occasional algal spores (figure 6).

Radular structure

Figure 7 shows SEM micrographs of an *S. pectinata* radula. Figure 7a,b show the anterior view and figure 7c,d show the posterior view. The anterior portion was convex in real life, and split slightly when flattened on the stub. The rest of the radula was rolled into a tube. The teeth on the anterior portion were small and did not appear mineralised. There was a small central tooth present.

Gut content analysis

The gut contents of foraging limpets consisted mainly of unidentifiable detritus and some inorganic material. The gut contents of animals collected in August 1994 contained small strands of a filamentous algae (figure 8) and algal spores (figure 9). It was not possible to identify the filamentous alga but it was probably a type of blue-green alga. The gut

Table I. Composition of the microbial film in grazed areas at the North Mole site. (√) indicates alga present

Date	*Blidingia* spp.	*Bangia* spp.	Filamentous blue-green	*Calothrix* spp.	*Ralfsia* spp.	Spores
Aug 93						
Oct 93	√		√			
Nov 93						
Dec 93		√	√			
Jan 94		√				√
Feb 94	√		√			√
Mar 94		√		√		
May 94			√		√	
Jun 94						
Jul 94						
Aug 94						
Oct 94	√	√	√			
Nov 94						√
Dec 94	√		√			
Jan 95		√				√
Feb 95			√			√
Mar 95			√			
Apr 95				√		
Jun 95						
Jul 95					√	
Aug 95				√		

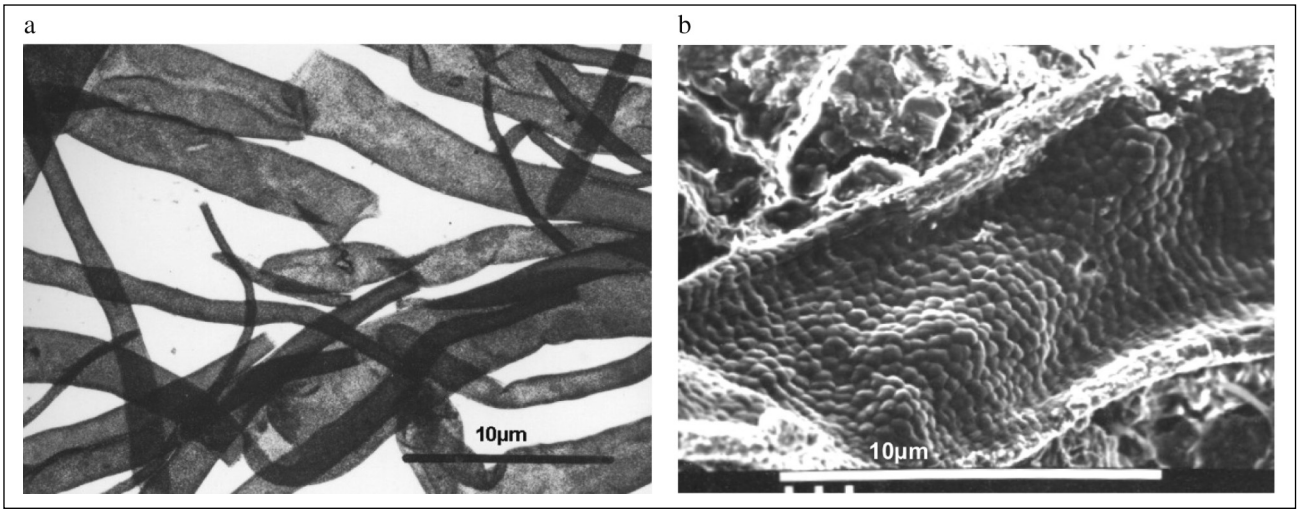

Figure 1. Fragments of juvenile *Blidingia* spp. (a): under the light microscope; (b): under the scanning electron microscope

contents of animals collected in October 1994 yielded some algal spores. At no other time was any algal form or spore observed in the gut contents of the animals collected at each census.

Faecal pellet analysis

There was no evidence of diatom silicaceous frustules present in the faecal pellets examined. *S. pectinata*'s faeces contained what appeared to be detritus and unidentifiable inorganic matter.

DISCUSSION

The low abundance of algae observed in rock chips and slurries derived from toothbrushings and scrapings of grazed areas on the upper midlittoral zone at the North Mole site suggests that in the

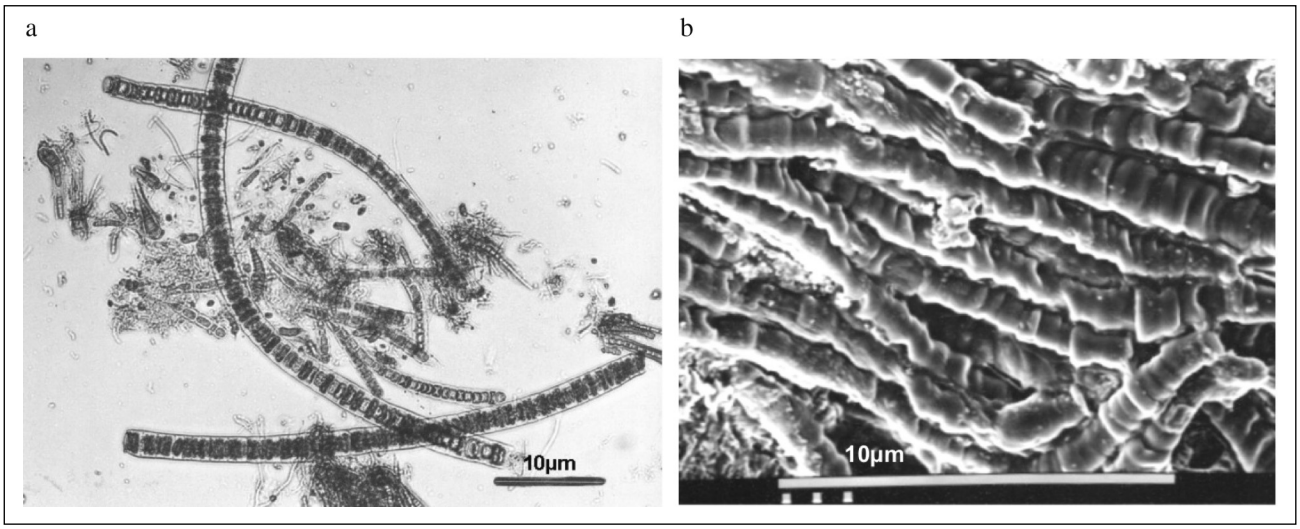

Figure 2. Fragments of *Bangia* spp. (a): under the light microscope; (b): under scanning electron microscope

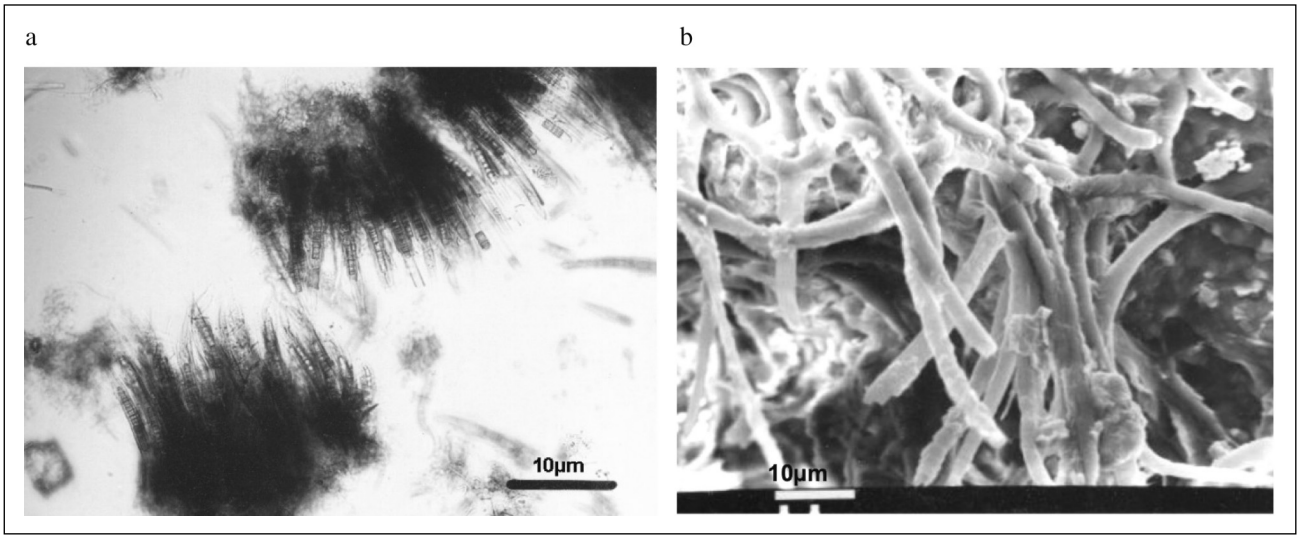

Figure 3. Fragments of juvenile *Calothrix* spp. (a): under the light microscope; (b) under the scanning electron microscope

presence of the three most common herbivorous grazers, *Siphonaria pectinata*, *Patella caerulea* and *P. rustica*, microalgal distribution and abundance was patchy. This was found to be the case by Hawkins and Hartnoll (1983), Hawkins *et al.* (1989) and Hill and Hawkins (1990, 1991) for British shores and Della Santina *et al.* (1993) for Mediterranean shores. Such algae as are present have apparently, by chance, found temporary escape from grazing by herbivores.

The relatively small sampling area used in this investigation may also have contributed to the apparent scarcity of algae on grazed areas. Moreover, the successful removal of microflora by means of toothbrushings, as reported by MacLulich (1986) for sandstone shores, may not have been as successful on Gibraltar's hard and apparently heavily-grazed limestone boulders. This was considered to be the case on British shale and limestone shores by Hill and Hawkins (1991). They further concluded that this technique would also fail to include endolithic algae which would also be available to docoglossan grazers, such as *Patella*, which are capable of excavating the rock (Steneck and Watling, 1982; Hawkins *et al.* 1989).

The absence of macroalgae from grazed areas in the upper midlittoral zone indicates that *S. pectinata* must feed on elements of the microbial film.

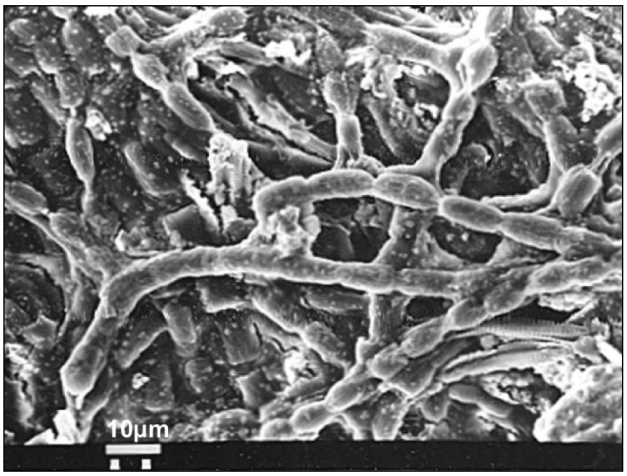

Figure 4. Scanning electron micrograph of unidentified filamentous green algae

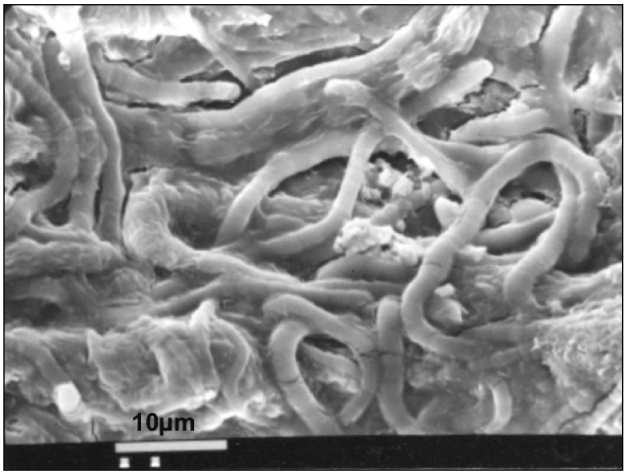

Figure 5. Scanning electron micrograph of unidentified blue-green algae

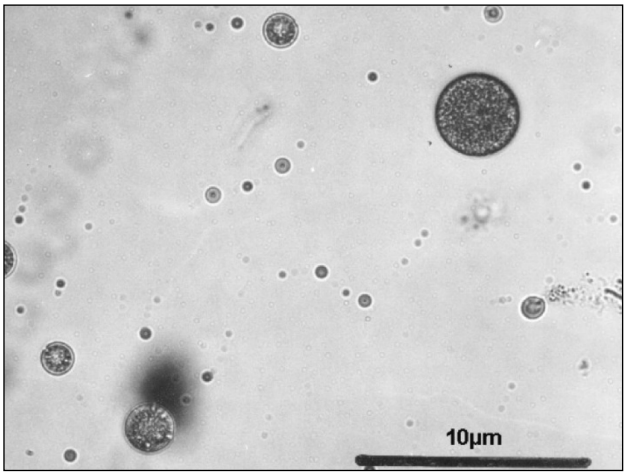

Figure 6. Light microscope photograph of algal spores

Considering this species's limited foraging range (Ocaña and Emson, 1999a), it is clear that much of the population will rarely, if ever, utilise macroalgae further down the shore as a food resource. The microbial film therefore appears likely to be providing sufficient food to support growth and reproductive activity (Ocaña, 1997; Ocaña and Emson, 1999b). It is difficult to state exactly which components of the microbial film are ingested by *S. pectinata*, particularly in view of the small amount of data provided by the gut contents analysis. It can be assumed that *S. pectinata* feeds on the spores and germlings of macroalgae and on patches of microflora (including filamentous blue-green algae) which have escaped grazing by other molluscs.

Our finding of large quantities of detritus in the gut of foraging animals suggests that *S. pectinata* is a generalist grazer which ingests a variety of material on the rock surface and extracts nutrients from the organic material it ingests. During the course of its grazing activities it presumably consumes microalgae, spores and germlings of any macroalgae which settle on the rock surface. This is evident from the analysis of gut contents showing fragments of a filamentous microalga (probably blue-green) and algal spores.

The problems involved in accurate descriptions of diet are not confined to the present study. For instance, Vadas (1985) considered that studies on the diet of herbivorous grazers were hindered by the difficulty of determining the microflora present in their gut contents and in establishing possible differences in the digestion rates of different algae. Hill and Hawkins (1991) reported that most gut material in limpets is digested rapidly, and analyses of gut contents are mainly limited to diatoms, whose silicaceous frustules are preserved indefinitely. Iwasaki (1993) noted that in grazed areas on Hong Kong's rocky intertidal zone, many *Cellana toreuma* individuals had little or no food in their guts, reflecting the absence of visible algae on the rock surface. This last observation parallels the situation at Gibraltar, where the small amount of food found in the gut contents of *S. pectinata* individuals may reflect the absence of macroalgae on grazed areas of the shore. The absence of diatoms from gut contents and faeces strongly suggests that they do not form part of *S. pectinata*'s diet, due to the high position on the shore occupied by this species.

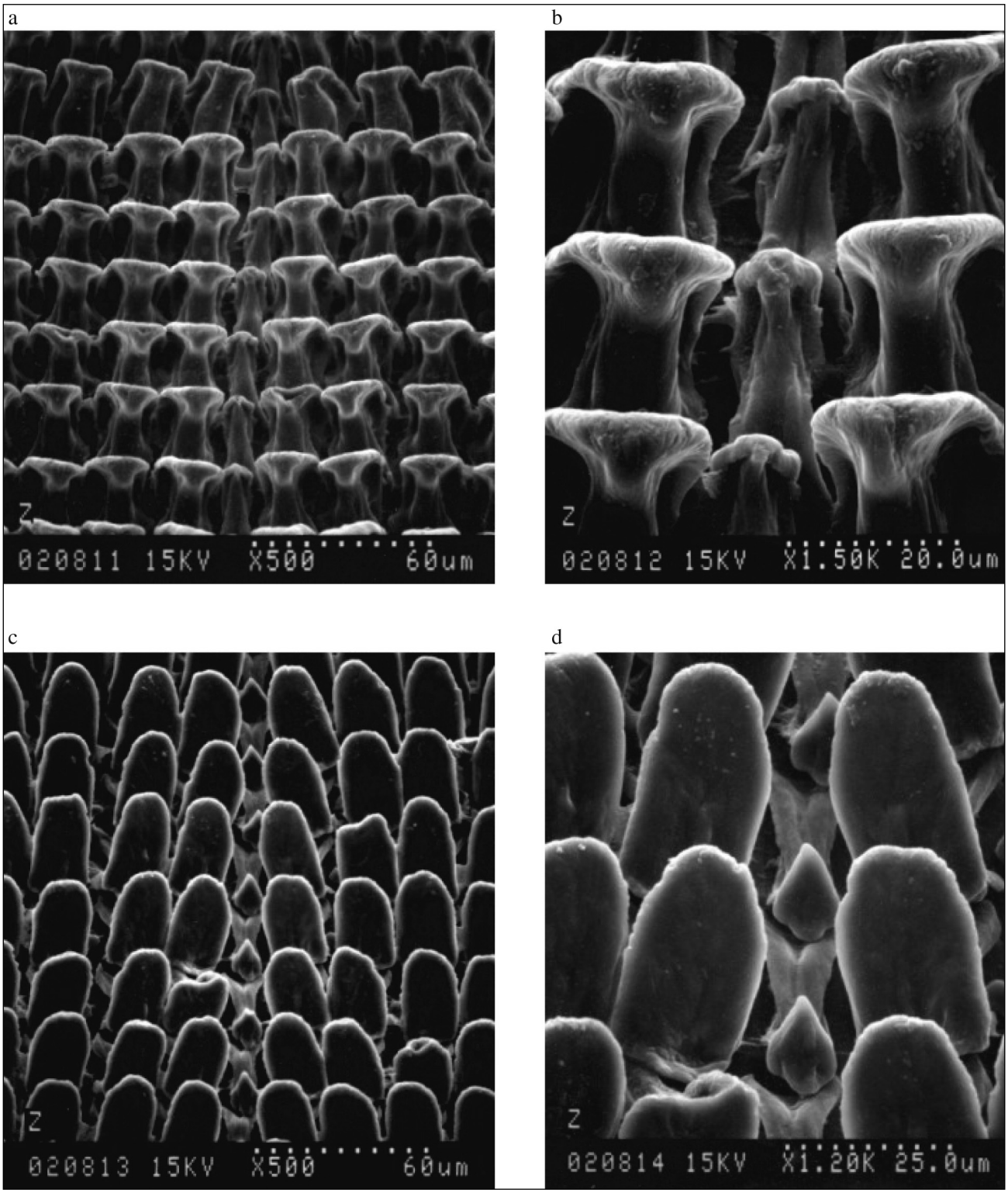

Figure 7. Scanning electron micrographs of *Siphonaria pectinata* radula. (a): anterior view (×500); (b): anterior view (×1 500); (c): posterior view (×500); (d): posterior view (×1 200)

This absence of macroalgae on grazed areas further indicates that the grazing activities of *S. pectinata* and coexisting Patellogastropods prevent the settlement and growth of macroalgae propagules by consuming spores and small sporelings. This effect has been reported by several authors; for instance

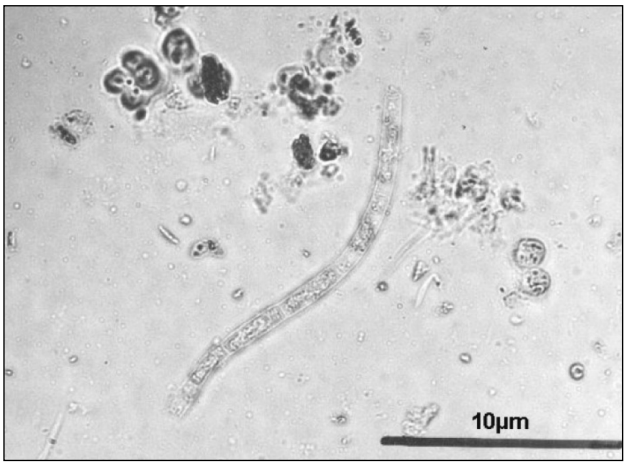

Figure 8. Filamentous algae extracted from gut contents of *Siphonaria pectinata*

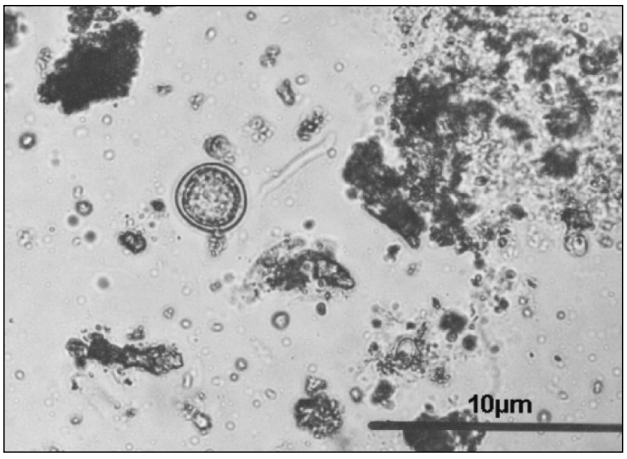

Figure 9. Algal spores extracted from gut contents of *Siphonaria pectinata*

Underwood and Jernakoff (1981) reported that the grazing activities of *Cellana tramoserica* prevented the colonization of macroalgae on rocky shores in New South Wales, Australia by consuming algae as they arrived as spores. Fernández and Miyares (1989) found that a characteristic feature of the *Chthamalus-Patella* zone on rocky shores in northern Spain was the absence of macroalgae. They concluded that this was due to the grazing activities of *P. vulgata*. Liu (1993) reported that the grazing activity of *Cellana toreuma* and *Patelloida saccharina* on the rocky intertidal of Hong Kong prevented the colonization of opportunistic ephemeral species by consuming their spores and early stages.

It is possible that *S. pectinata* exercises a degree of selectivity regarding what types of algae it ingests. In enclosures containing *S. pectinata* (Ocaña, 1997), the only algae present were crust-forming algae, such as *Calothrix* spp. and *Ralfsia* spp. Softer and frondose types, such as *Blidingia* spp. and *Bangia* spp., were absent, despite being very abundant in the grazer-free areas. This suggests that when present on the shore, *Blidingia* spp. and *Bangia* spp. are the main food resource utilised by *S. pectinata*. Such findings are consistent with those for other *Siphonaria*, which report a preference for softer, foliose algae rather than encrusting forms (Black, 1979; Branch, 1981; Underwood and Jernakoff, 1981; Creese and Underwood, 1982; Hawkins and Hartnoll, 1983; Black *et al.*, 1988; Beovich and Quinn, 1992; Iwasaki, 1993).

This apparent selectivity may be the result of *S. pectinata*'s radular structure. Several researchers have concluded that *Siphonaria*'s numerous small, non-mineralised teeth are more suited for rasping softer, frondose macroalgae from the rock surface (Creese, 1978; Black, 1979; Branch, 1981; Underwood and Jernakoff, 1981; Creese and Underwood, 1982; Hawkins and Hartnoll, 1983; Black *et al.*, 1988; Beovich and Quinn, 1992; Iwasaki, 1993). These authors consider that unlike the radulae of patellogastropod limpets, *Siphonaria* teeth are not particularly suited to excavating the rock surface and removing embedded microflora or tough encrusting algae and are unable to completely prevent colonisation and growth of macroalgae.

This may explain the presence of *Calothrix* spp. and *Ralfsia* spp. in *S. pectinata* only enclosures (Ocaña, 1997). The animal may be able to remove *Blidingia* spp. and *Bangia* spp. spores and germlings but may not be as successful when dealing with tough encrusting algae, such as *Calothrix* spp. and *Ralfsia* spp. Similar findings were reported by Beovich and Quinn (1992) and Iwasaki (1993) for two species of *Siphonaria*. In both cases *Siphonaria* was found to prevent colonisation and growth of foliose algae by removing juvenile thalli, but was unable to prevent settlement and growth of encrusting alga such as *Ralfsia* spp. It would appear that the radula of *S. pectinata*, although lacking in the excavating properties of patellogastropod radulae, is nevertheless capable of removing many components of the microbial film.

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